A New Species of *Bunnya* (Gastropoda: Pulmonata: Humboldtianidae) from Western Mexico, with Notes on its Life Cycle and Familial Relationships

by

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Abstract. A new species of land snail, Bunnya naranjoae Miller, is described from western Mexico. Its unusual life cycle of about one year from birth to maturity, with death after egg laying, is described. Its anatomy places it in the family Humboldtianidae, formerly considered a subfamily of Helmintho-glyptidae and recently elevated to familial rank by A. A. Schileyko.

INTRODUCTION

BAKER (1942) described the genus Bunnya and its type species, Bunnya bernardinae H. B. Baker, 1942, from a single specimen collected on the wall of the old monastery at El Desierto de los Leones at the western outskirts of Mexico City. Since that time, B. bernardinae has also been collected by Gonzalo Halffter at Temexcaltepec, Estado de Mexico, and by my graduate student Edna Naranjo Garcia in lower elevations of the Desierto de los Leones, Distrito Federal. Baker stated that "in its genitalia, Bunnya appears to approach Humboldtiana," but he felt that its shell and external body characters related it closely to Xanthonyx Crosse & Fischer, 1867. Accordingly, he did not place it in a designated family but merely referred to it as "a new genus of Mexican helicids."

BAKER (1959) subsequently discussed the use of the family names Xanthonychidae, Helminthoglyptidae, Bradybaenidae, and others which have been used for dartbearing helicoids whose mucus glands are "club-shaped, globular, or irregular (not tubular or finger-shaped)" (PILSBRY, 1939:1). He concluded that because the name Xanthonychidae has priority over the others, it "must be accepted for at least the native American genera of helicoids" (BAKER, 1959:28); he went on to state that "since the sizes of families are matters of convenience and/or custom, we Americans, North and South, can leave to the wisdom of our Old World colleagues the advisability of a separate family for the genera of their home lands." Indeed, Old World genera belonging to this group of helicoids have been placed in Bradybaenidae, effectively separating them from New World genera.

Baker's recommendation that the name Xanthonychidae be adopted in lieu of the better known name Helminthoglyptidae did not meet with universal acceptance. SOLEM (1983:47) stated that he did not "accept strict nomenclatural priority for names of families and higher level taxa." A. A. Schileyko, in his extensive analysis of the evolution and relationships of pulmonate gastropod mollusks (SCHILEYKO, 1973, 1978, 1979), also continued to use the name Helminthoglyptidae. In his 1978 study of the superfamily Helicoidea based on detailed anatomical characters, he raised the Humboldtianinae Pilsbry, 1939, to familial rank, thereby also separating that group of helicoids from the Helminthoglyptidae. His determinations were summarized in an evolutionary tree (SCHILEYKO 1979:60-61, figure 7) showing the Humboldtianidae in the direct evolutionary line from a common helicoid ancestor, with the Helicidae branching off at an early date, the Helminthoglyptidae at a later date, and the Bradybaenidae branching off at a still later date from the Helminthoglyptidae. He placed these families in the superfamily Helicoidea, named in accordance with Article 29a of the International Code of Zoological Nomenclature.

Pilsbry's Humboldtianinae was a monogeneric subfamily consisting only of the genus *Humboldtiana* Ihering, 1892. ZILCH (1960) added *Lysinoe* H. & A. Adams, 1855,



Figure 1

Shell of holotype of Bunnya naranjoae, spec. nov. SBMNH No. 34369. Dorsal, ventral, and side views.

to the subfamily. I now report that a new species of the genus Bunnya, described below, provides additional evidence that this genus is more closely related to Humboldtiana than to Xanthonyx and should therefore be placed in the family Humboldtianidae. I concur with Schileyko that the Humboldtianidae are sufficiently distinct anatomically from other Helicoidea to warrant their status as a separate family. The names used here for taxa above the family level also follow his recommendations (SCHILEYKO, 1979).

SYSTEMATICS

Subclass Pumonata Superorder Stylommatophora Order Geophila Suborder Helixina Superfamily Helicoidea Family Humboldtianidae Genus Bunnya H. B. Baker, 1942

Bunnya naranjoae Miller, spec. nov.

(Figures 1, 2)

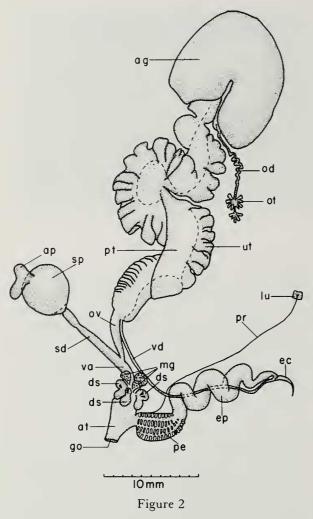
Diagnosis: A sluglike land snail with thin, fragile, depressed, vitriniform shell, overlapped all around by a papillose fold of the mantle, too small to contain entirely the retracted animal. The reproductive system is characterized by 3 bilobed dart-sacs and 3 saccular mucus lands arranged circumferentially around the vagina near the genital orifice, by an epiphallus tightly coiled around the vas deferens, and by a short-ducted spermatheca equipped with a globular appendix at its apex.

Description of shell of holotype: Shell imperforate, thin, fragile and translucent, slightly glossy, light brown colored, vitriniform, with only 2³/₄ whorls, depressed, rounded, and rapidly increasing in size. Embryonic whorls 1¹/₄, sculptured with very closely set, parallel, spiral grooves (about 40 per mm) superimposed on closely set radial

riblets (about 10 per mm at lower suture); spiral grooves sparse and widely scattered on subsequent whorls, while radial riblets continue closely set to the end of the second whorl, thereafter becoming more widely spaced, irregular, and weakly rounded. On top of the body whorl, an ovoid, irregular callus marks where the edge of the mantle fold overlapped the shell. Aperture large, ovoid, oblique, much wider than high, in plane about 120° from the shell axis; peristome sharp and thin, very fragile; parietal callus somewhat thick, glossy and granular. Columella sharp, thin and arcuate. Shell diameter 18.0 mm, height 11.3 mm; number of whorls 2¾.

Variation in shells of paratypes: Seventeen paratypes had shells that were measurable, having been obtained from freshly killed specimens; shells from dead specimens were generally decalcified, shrivelled, and partially broken. The smallest measurable adult shell had a diameter of 17.0 mm while the largest measured 18.9 mm; the mean was 17.9 mm. Shells had variable amounts of callus deposit on top of the body whorl, marking variable degrees of overlap by the mantle fold; in some shells, the embryonic whorls were completely covered by thick callus. Except for the callus deposits, the shells varied from glossy to dull brown; one shell was light lemon yellow.

Anatomical features: Living animals varied from dark gray to pale brown. All but one, out of 18 live adults, possessed a prominent tail horn; the hornless individual showed no vestige whatsoever of a horn. In some specimens, the body wall at the edge of the foot, as well as on the back of the tail, was colored a pale chartreuse, while in others the color was orange. The mantle edge overlapped the shell all around, to varying degrees, usually including the spire, and secreted a calcareous callus; as the mantle protracted and retracted, the callus tended to form a solid sheet, covering large portions of some shells. In one specimen, the mantle had overlapped the shell entirely and its edges had fused, thereby effectively creating



Reproductive system of *Bunnya naranjoae*, spec. nov. Drawing made from projection of stained whole mount, WMB 7473; specimen collected in Sierra de Manantlan, Jalisco, Mexico, along road from El Chante to Guizar, 16 km south of El Chante, by E. Naranjo Garcia & W. B. Miller, 26 Dec. 1984. Abbreviations: ag, albumen gland; ap, appendix of spermatheca; at, genital atrium; ds, dart-sac; ec, epiphallic caecum; ep, epiphallus; go, genital orifice; lu, portion of floor of lung; mg, mucus gland; od, oviducal duct (hermaphroditic duct); ot, ovotestis; ov, oviduct; pe, penis; pr, penial retractor; pt, prostate; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens.

an internal shell. The mantle overlap was coarsely papillose and pigmented with irregular, black, radial lines. The thin mantle directly over the viscera, under the shell, was maculated with scattered pigment spots around the anterior and lateral edges; the maculae coalesced to form a connected, reticulate pattern over the heart and the white kidney; the mantle over the digestive gland and the ovotestis was clear, without pigment. A dark pigmented groove led from the pneumostome to the mantle edge at the apex of the spire.

The anatomy of the reproductive system (Figure 2) is generally similar to that of Bunnya bernardinae in that there are three bilobed dart-sacs located circumferentially around and opening into the vagina at a point about 6 mm posterior to the genital orifice. There are also three saccular, globose, mucus glands just posterior to the dartsacs, each with its own duct descending into the vagina at the level of, and between, each dart-sac. In 14 specimens dissected, some had two darts per sac, others had only one, and still others had none. The globose spermatheca has an appendix situated at its apex, somewhat ear-shaped or bilobed, and a relatively short (ca. 8 mm) spermathecal duct without diverticulum. The penis is short, bulbous (5 mm long and 3 mm in diameter) with its inner wall consisting of numerous, small, rectangular, glandular alveoli arranged in a reticulate pattern clearly visible on the outer surface. Posteriorly, the lumen of the penis leads into a tightly coiled epiphallus wound helically around the vas deferens, forming from 21/2 to 31/2 coils; the lumen of the epiphallus is lined with five or six prominent longitudinal pilasters for its entire length; there is a short epiphallic caecum, about 3-4 mm in length. The penial retractor muscle is extremely thin, long, and attached to the penis. The vagina, in the region of the mucus glands and dartsacs, is attached by numerous thin strands of connective tissue to the right lateral body wall; its lumen is lined with from 10 to 15 anastomosing longitudinal pilasters. The widely convoluted uterus and prostate, the lobed albumen gland, and the ovotestis of clavate alveoli are as in B. bernardinae.

Disposition of types: Holotype: Santa Barbara Museum of Natural History no. 34369. Paratypes: U.S. National Museum no. 859016; Academy of Natural Sciences of Philadelphia no. 360102; Field Museum of Natural History no. 205901; California Academy of Sciences no. 060385; University of Texas at El Paso no. 9386; Florida State Museum no. 80271; Universidad Nacional Autonoma de Mexico (UNAM) no. 1020; Edna Naranjo García Collection no. 526; W. B. Miller (WBM) no. 7473.

Type locality: Sierra de Manantlan, Jalisco, Mexico; along road from El Chante to Guizar, 1.5 km (0.9 mi) south of Rancho Manantlan (or 16 km south of El Chante), under large rocks between road and left bank of Rio Manantlan; 19°36.5'N, 104°12.3'W, elev. ca. 1390 m (4550 ft).

Distribution and habitat: This species appears to be wide ranging along the tropical areas of the western slope of the Sierra Madre Occidental from the vicinity of Mazatlan in the north to the Sierra de Manantlan in southwest Jalisco. Areas farther south and east, in Colima, Michoacan, *etc.*, have not been explored for this species. At its northernmost known locality, a ravine along the Mazatlan-Durango highway 3 km easterly from Santa Lucia (or 15 km westerly from Loberas summit), I obtained several shells and a live adult in December 1962; dissection of the adult anatomy confirmed its identity (no. WBM 4401). Another locality in Nayarit, a ravine along the Tepic-Puerto Vallarta highway at km-42 marker (measured from Tepic), yielded a single shell in January 1973 (no. WBM 6068). In the Sierra de Manantlan, it is found under rocks, especially rock piles from crumbling rock walls, in the riparian valley of the Rio Manantlan, from the type locality (1.5 km south of Rancho Manantlan) to the vicinity of the abandoned sawmill at Rincon de Manantlan, 1.1 km farther upstream along the river. The dominant trees along the river banks are large alders (*Alnus* sp.), several leguminous trees, a large-leaf oak (*Quercus* sp.), and an occasional five-needled yellow pine.

Comparative analysis: Bunnya naranjoae differs from the only other described Bunnya, B. bernardinae, by its shell which is larger and flatter and by its reproductive anatomy which has a multicoiled epiphallus and a spermathecal appendix, situated at the apex of the spermatheca, instead of a spermathecal diverticulum below the spermatheca, as reported by Baker for B. bernardinae.

Etymology: This species in named for my graduate student, M-en-C Edna Naranjo Garcia, whose tireless search and keen eyesight resulted in the discovery of the numerous, minute, live, embryonic specimens that enabled me to study their life cycle as well as obtain, eventually, large numbers of adult animals for dissection.

LIFE CYCLE

Bunnya naranjoae has a most unusual life cycle in that it lives only for one year, hatching near the end of the rainy season, hibernating in its embryonic shell tightly sealed to rocks during the dry season, and then activating and rapidly growing to adulthood during the next rainy season, at the end of which it lays eggs and dies. When first found by Edna Naranjo Garcia, on 26 December 1984, the specimens had only tiny embryonic shells (ca. 3 mm in diameter) and were hibernating, strongly sealed to the underside of large rocks in rock piles. In obtaining two to three dozen specimens, it was impossible to avoid crushing some shells while trying to pry them off the rocks. The young snails were immediately activated in terraria at the UNAM Biological Field Station at Chamela, Jalisco. The terraria were provided with a layer of humus, dead leaves, and stems from the type locality in the event that certain essential food items might occur there; later, however, additional terraria were established, with different forest litter, and no apparent ill effects were noted. The snails were fed fresh romaine lettuce every three or four days, with sliced carrots added occasionally. They ate ravenously, grew rapidly in size, and by April, about four months after activation, they reached adulthood. In early May, some individuals began to die, and large clutches of eggs (25 to 30 eggs each) appeared in the litter. Moribund, emaciated snails lay near the egg masses, with prolapsed genital atrium and shrivelled shell largely devoid of calcareous material, as in *Vitrinizonites uvidermis* Pilsbry, 1890. On dissection, it was found that the albumen gland had atrophied and the uterus and spermatheca were lysing. Apparently, the process of forming and laying such large numbers of eggs had robbed the animal of excessive quantities of tissue, nutrients, and minerals. Young snails soon hatched, in about two or three weeks, with strong, ribbed, embryonic shells. At that time, the terraria were allowed to dry out, to simulate a dry season, and the young snails promptly sealed to the walls with strong, calcareous epiphragms. This short life cycle of one rainy season activity explains why no live adults could be found during the dry season and why most dead shells were thin, fragile, and damaged.

FAMILIAL RELATIONSHIP

The shells of Bunnya naranjoae collected in 1962 and again in 1973 were originally thought to be a species of Xanthonyx. Likewise, the specimens from the Sierra de Manantlan were thought to belong in the genus Xanthonyx because their appearance in size, shape, and form resembled published descriptions of species of Xanthonyx. Dissection, however, revealed that the anatomy was unquestionably that of Bunnya.

Although the shell of Bunnya naranjoae is similar to that of Xanthonyx spp., this similarity is considered another example of convergent evolution. In numerous instances, reduced, sluglike shells of similar appearance have been shown to belong to animals whose dissimilar anatomy places them in entirely different families, e.g., Binneya Cooper, 1963, in Arionidae, Gaeotis Shuttleworth, 1854, in Bulimulidae, and Vitrinizonites W. G. Binney, 1879, in Zonitidae. LIKHAREV & WIKTOR (1979) reported on an extensive and detailed analysis of parallelism in the structure of slugs and sluglike snails.

Anatomically, Xanthonyx is known only from three of the five described species, and in each of these, the reproductive anatomies are significantly different. In X. sumichrasti (Brot, 1867), the type species of the genus, FISCHER (1867) showed one mucus gland, no dart-sac, and a spermathecal diverticulum; in X. cordovanus (Pfeiffer, 1856), BAKER (1942) reported two "dart-glands with a few tubules" entering the vagina above a rudimentary dart-sac, and a spermathecal diverticulum; in X. salleanus (Pfeiffer, 1956), PILSBRY (1900) showed two mucus glands, one dart-sac, and no spermathecal diverticulum. The anatomies of X. chiapasensis (Pfeiffer, 1956) and X. potosiana Dall, 1907, have not been reported in the literature, to my knowledge. Fred G. Thompson (in litt., 1985) reported that he had an undescribed species from San Luis Potosi whose dart-glands and dart-sacs are sufficiently different from typical Xanthonyx, as described by Strebel, to warrant recognition of a new genus. He added, however, that we know too little about xanthonychid systematics to justify the hasty designation of a new genus for that particular species. It appears obvious that much more work

needs to be done to collect live adult topotypes of the described species of *Xanthonyx* in order to study their anatomies and obtain reliable data on which to base satisfactory determinations of their systematic relationships.

In Bunnya naranjoae, however, the generic characteristics, namely the arrangement, shape, and position of the three bilobed dart-sacs and three mucus glands, are virtually identical with those of *B. bernardinae*. These characteristics, while establishing concise criteria for generic identity, also indicate a close evolutionary relationship with *Humboldtiana* whose four saccular mucus glands and four dart-sacs are arranged circumferentially around the vagina in a similar manner as in Bunnya. Accordingly, the genus Bunnya is here placed in the family Humboldtianidae.

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LITERATURE CITED

- BAKER, H. B. 1942. A new genus of Mexican helicids. Nautilus 56(2):37-41.
- BAKER, H. B. 1959. Xanthonychidae (Pulmonata). Nautilus 73(1):25-28.
- FISCHER, P. 1867. Anatomie de deux mollusques pulmones terrestres appartenant aux genres Xanthonyx et Hyalimas. J. de Conch. 15:213-221.
- LIKHAREV, I. M & A. WIKTOR. 1979. Parallelisms in the structure of slugs of the superorder Stylommatophora and their systematic position. *In:* Morphology, systematics and phylogeny of mollusks. Acad. Sci. USSR, Proc. Zool. Inst. 80:70-86.
- PILSBRY, H. A. 1900. Metostracon, a new slug-like genus of dart-bearing Helicidae. Proc. Malacol. Soc. Lond. 4:24-30.
- PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Phila., Monogr. (3)I(I):ixviii + 1-573 + i-ix; figures A, B, 1-377.
- SCHILEYKO, A. A. 1973. Comparative characteristics of Palaearctic families of terrestrial molluscs from the superfamily Helicoidea. Acad. Sci. USSR, Zool. Mag., 1973, 52(4): 492-506.
- SCHILEYKO, A. A. 1978. Land mollusks in the superfamily Helicoidea. In: Fauna of the USSR, Mollusks 3(6). Acad. Sci. USSR, Zool. Inst. 384 pp.
- SCHILEYKO, A. A. 1979. The system of the order Geophila (Helicida) (Gastropoda Pulmonata). In: Morphology, systematics and phylogeny of mollusks. Acad. Sci. USSR, Proc. Zool. Inst. 80:40-69.
- SOLEM, A. 1983. Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra) Part II: families Punctidae and Charopidae, Zoogeography. Field Museum of Natural History, Chicago, Illinois. 336 pp.
- ZILCH, A. 1960. Gastropoda: Euthyneura. In: Handbuch der Palaozoologie. Band 6, Teil 2, Lief 4:601-834, figures 2112-2515.